



Juvenile gadoid habitat and ontogenetic shift observations using stereo-video baited cameras

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ABSTRACT: The protection of species requires an understanding of their habitat requirements and how habitat characteristics affect their distribution, survival and growth. This need is especially important in areas where anthropogenic pressures can not only have a significant direct impact on the survival of the species but also damage their habitat. The Firth of Clyde in south-western Scotland was an important commercial fishing area for a variety of demersal fish species up until 1973. However, stocks rapidly declined thereafter and the catch of targeted species ceased in 2005, despite fisheries measures put in place to aid recovery. Changes in the availability and quality of fish habitat are possible explanations for this lack of recovery. Here, we report on stereo baited remote underwater video surveys in the Firth of Clyde between June and September in 2013 and 2014 to determine the habitat of juvenile Atlantic cod *Gadus morhua*, haddock *Melanogrammus aeglefinus* and whiting *Merlangius merlangus*. Habitat predictor variables explored included substratum type, depth, wave fetch, and epibenthic and demersal fauna diversity. *G. morhua* were most abundant in shallow, sheltered areas composed of gravel–pebble containing maerl. *M. aeglefinus* and *M. merlangus* predominated over deeper sand and mud. Ontogenetic shifts in all 3 species were also observed. Relative abundances of *G. morhua* and *M. merlangus* were positively related to the diversity of epibenthic and demersal fauna. Our results indicate that spatial conservation measures to benefit demersal fish should be advised by patterns of epibenthic and demersal fauna diversity as well as physical substratum types.

KEY WORDS: Nursery · Habitat association · Ontogenetic shift · Gadoid · Diversity · Atlantic cod · *Gadus morhua* · Density dependence · Stereo-video camera

INTRODUCTION

With increasing pressures on marine ecosystems and little recovery being observed in commercially important fish, it is essential to understand the factors affecting their survival. Unfortunately, in many cases, the habitat requirements of commercially important stocks are often not well understood. Atlantic cod *Gadus morhua*, haddock *Melanogrammus aeglefinus* and whiting *Merlangius merlangus* are of considerable economic importance throughout the North Atlantic (Cote et al. 2003, Fernandes & Cook 2013). However, stocks of all 3 species declined in the late

20th century (Holmes et al. 2014, ICES 2016a,b,c). Efforts have been put in place to recover these stocks, but little progress has been observed in much of the west coast of the UK, and recruitment and spawning stock biomass remains relatively low in that area for all 3 species (Fernandes & Cook 2013, ICES 2016a,b,c). This is especially the case in the Firth of Clyde (southwest Scotland), where the demersal fishery was predominant (Thurstan & Roberts 2010, Heath & Speirs 2012)

The recovery of commercial fish species depends not only on reductions in targeted fishing and by-catch but also on healthy recruitment of juvenile fish.

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To facilitate recruitment, juveniles need access to adequate food resources and shelter to minimise natural mortality and maximise survival and growth (Beck et al. 2001, Elliott et al. 2016b). Few studies have looked at the quality of the seabed indicated by epibenthic and demersal fauna diversity (mobile epibenthic fauna and demersal fish species). Understanding juvenile gadoid habitat is particularly important given that settlement and post-settlement survival is thought to be the best means to understanding gadoid population regulation (Myers & Cadigan 1993, Olsen & Moland 2011, Laurel et al. 2016). Furthermore, many species undergo ontogenetic shifts and may require more complex management measures for protection (Fitzpatrick et al. 2012, Nagelkerken et al. 2013).

For clarification purposes, the understanding of habitat refers to the substrata (abiotic and biotic seabed characteristics), physicochemical and biological characteristics required by a species to survive during a particular stage in its ontogeny (Elliott et al. 2016b). An important habitat component is one which a change in its condition or availability may directly affect the species success (e.g. survival or growth) (Gibson 1994, Able 1999, Elliott et al. 2016b). Terms outlined within Elliott et al. (2016b) have been used to improve understanding of the relationship between juvenile gadoids and their habitats. Many studies that have looked at the habitat use of these gadoids have not considered biological characteristics, such as how other species may affect abundance observations (e.g. Tupper & Boutilier 1995a, Bertelli & Unsworth 2014, Seitz et al. 2014). This is most likely due to the difficulties of quantifying biological characteristics and interactions using traditional trawl survey methods (Lima & Dill 1990, Able 1999).

Structurally rugose substrata, such as cobbles, kelp beds and seagrass, provide refuge from predators for juvenile *G. morhua* (Gotceitas & Brown 1993, Gotceitas et al. 1995, Tupper & Boutilier 1995a). However, if these substrata become saturated from increased juvenile gadoid abundance, juveniles may be forced into lower-quality areas where survival is likely to be lower (Morris 1989, 2003, Laurel et al. 2004). Equally, areas of higher biodiversity may provide increased food sources in addition to refuge (Sebens 1991, Gratwicke & Speight 2005, Kovalenko et al. 2012). Few *in situ* studies have been undertaken to explore *M. aeglefinus* and *M. merlangus* substratum association.

The majority of fish distribution and abundance surveys around the UK, and more widely, have taken place through trawl and egg surveys (Vasconcelos et

al. 2014) (e.g. Gibson et al. 1996, Wright et al. 2010, Bastrikin et al. 2014). Such methods provide little information on fine-scale substratum associations that may affect gadoid distribution (e.g. Gregory & Anderson 1997, Gorman et al. 2009). Photogrammetric techniques can provide a useful means of collecting non-damaging and non-extractive data on fish, epibenthos and substrata (Harvey et al. 2007, Fitzpatrick et al. 2012, Elliott et al. 2016a). Data collection using imaging enables access to shallow and structurally rugose seabed types, and protected areas that would otherwise be inaccessible using trawl or seine netting methods (Cappo et al. 2006).

Stereo imaging systems are particularly advantageous as they enable accurate measurements to be made from stills or video (Harvey et al. 2002). Baited cameras are commonly presumed to be biased towards larger predators and scavengers (Lowry et al. 2012, Dunlop et al. 2015). However, comparisons between baited and unbaited cameras have shown higher relative abundances and species diversity in baited camera observations (Watson et al. 2005, Harvey et al. 2007, Bernard & Götz 2012). Stereo baited remote underwater video (SBRUV) surveys may be part of the solution to the survey and monitoring requirements of spatial management in the UK.

The aims of this study were to identify the environmental variables (including 5 seabed types, epibenthic and demersal fauna diversity through Shannon-Wiener entropy, depth and wave fetch) that juvenile gadoids are associated with, and to describe their habitat using SBRUV deployments. By understanding the habitat variables affecting the distribution and growth of juvenile gadoids, multi-purpose protection measures can be proposed to protect not only vulnerable benthos of conservation importance but also commercially valuable gadoids.

MATERIALS AND METHODS

Study area

Data were collected within the South Arran Nature Conservation Marine Protected Area (NCMPA) at depths of 4.0–47.2 m (Fig. 1). The NCMPA was designated in 2014 for its seagrass and maerl beds (coralline red algae *Phymatolithon calcareum*) in addition to burrowed mud, kelp and seaweed communities and epibenthic fauna (www.snh.gov.uk/protecting-scotlands-nature/protected-areas/national-designations/mpas), and encompasses an area of 250 km². Data were collected between June and Sep-

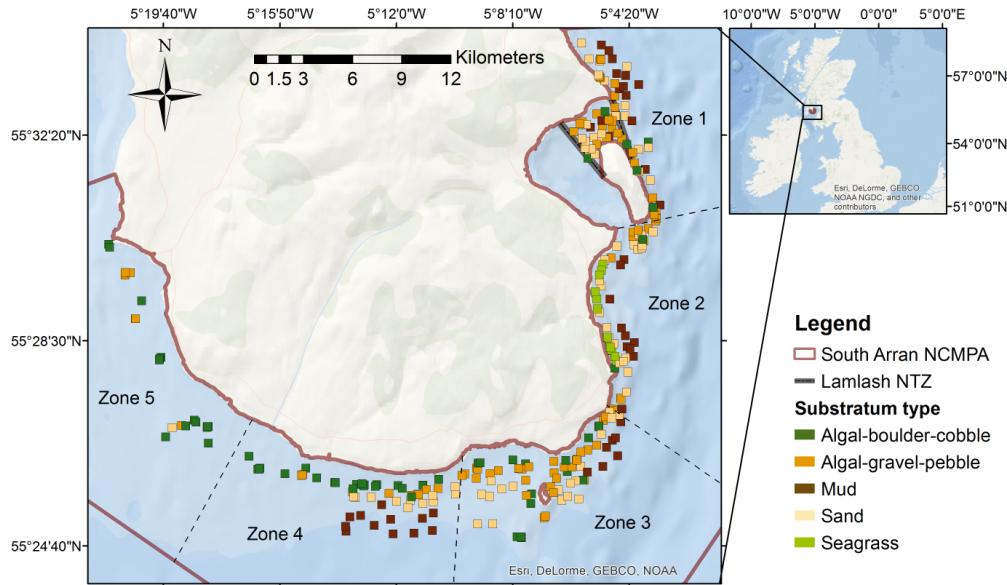


Fig. 1. Stereo baited remote underwater video (SBRUV) deployment locations within South Arran Nature Conservation Marine Protected Area (NCMPA) and Lamlash no-take zone (NTZ) over the course of 2013 and 2014. Different coloured squares represent the different substratum types observed

tember 2013 and 2014, but took place before management measures were implemented. Within the NCMPA, the Lamlash Bay no-take zone (designated in 2008) covers an area of 2.67 km², where all commercial and recreational fishing is prohibited within its boundaries (Thurstan & Roberts 2010).

Data collection

In the sampling design, the NCMPA was divided into 5 zones, with samples collected within each zone over the period of data collection to facilitate replication. These zones differed in wave fetch (Burrows et al. 2008) and substratum type (following the collation of existing information from locals and broad-scale predicted seabed maps). Stratified random sampling location points within each zone were generated using Geospatial Modelling Environment software (version 10.1, <http://spatialecology.com/>). Deployment locations varied slightly between years due to logistical reasons (during field season 2013 a 6.5 m RIB was used; during field season 2014 a slower-speed, larger 10.8 m research vessel was used). For 2013, 74 deployments were conducted between 5 June and 29 September. However, only data collected after 15 July were used due to the late arrival of gadoids. During 2014, 186 deployments were conducted from 30 June to 18 September in 4 time periods (for boat time efficiency) during the course of the summer.

Three baited camera systems were used, each consisting of a pair of high-definition Canon (HF G25) video cameras in waterproof housings (SeaGIS, www.seagis.com.au/). The cameras were mounted on a 57-cm-high custom made steel frame (Fig. 2), angled at an ~15° oblique view to have a partial view of the seabed and an inward angle of approximately ~8° with a basal separation of 58 cm. Each camera was set to manual mode with the focal length set to

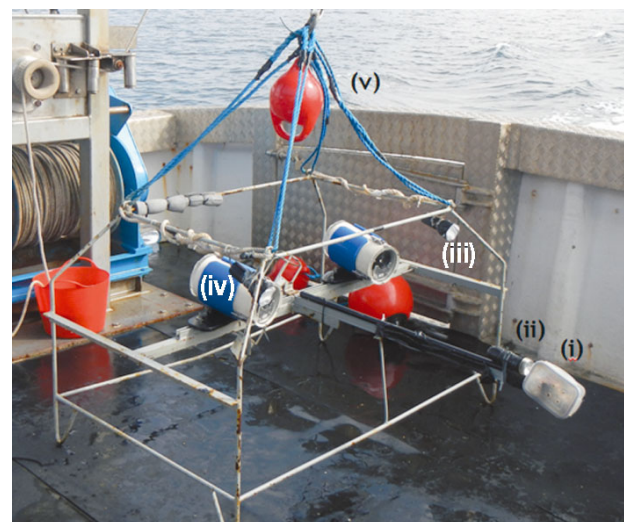


Fig. 2. Stereo baited remote underwater video system showing (i) bait box, (ii) strobe to synchronise cameras, (iii) torches, (iv) waterproof housing containing video cameras and (v) float and ropes to deploy the frame to the seabed from the vessel

infinity (∞). Two underwater, LED W38VR Archon-light (1400 lumen) torches were mounted on the frame, facing at an angle to the middle of the stereo-camera field of view. A flashing strobe and bait box was attached on a 91-cm-long bait arm situated in front of the camera. The strobe was used to synchronise the stereo-video images. Bait consisted of 500 g of cut Atlantic mackerel *Scomber scombrus*. The SBRUV frame was tethered to a rope for deployment and retrieval.

The system was set up in a similar way to the prototype described in Harvey & Shortis (1995, 1998). However, our system was optimised for smaller-bodied (<50 cm) fish in seawater with a visibility of <6 m distance by bringing the cameras closer together. The maximum depth and width of the field of view at which gadoids could be measured was 4 m \times 2 m. Prior to and over the course of field data collection, the mounted cameras were calibrated within a controlled environment using the methods outlined in Harvey & Shortis (1998) and CAL software manual (version 2.11, www.seagis.com.au/event.html).

Camera systems were deployed for a minimum of 55 min on the seabed. This deployment length provided the best compromise between sufficient bait soak time for species accumulation, as tested by Unsworth et al. (2014), and the need to bait and redeploy each camera multiple times on each sampling day. To minimise the possibility of deployments affecting each other, SBRUV deployments on the same day were a minimum distance of 500 m apart to minimise the possibility of juveniles swimming between SBRUV deployments. Samples were collected between 09:00 and 15:00 h (GMT), so that all deployments would be a minimum of 3 h after sunrise and 3 h before sunset to avoid crepuscular variation in fauna behaviour (e.g. Keats & Steele 1992, Bertelli & Unsworth 2014).

Video analysis

Each deployment was analysed using Event Measure software (version 3.42, www.seagis.com.au/event.html) and a sample of 48 deployments were analysed by 2 separate observers to check for observer bias. All epibenthic and demersal fauna identified were quantified to the lowest taxonomic level possible. The maximum number of individuals of the same species appearing in a frame at the same time (MaxN) was used as a measure of relative abundance (Priede et al. 1994, Watson et al. 2005, Cappo et al. 2006). MaxN avoids repeat counts of individuals re-entering the field of view (Priede et al. 1994, Watson et al. 2005).

For gadoid length measurements, each individual observed had to be visible in both cameras. Fish fork length measurements were taken at one time point per deployment, when the maximum number of measurable fish was present. All length measurements with a root mean square (RMS) error >2 cm and a precision of length measurement >0.5 cm were removed from the analysis.

To undertake seabed-type categorisation, still images were extracted from the video recordings. Coral Point Count (CPC) analysis (version 4.1; Kohler & Gill 2006) was used to record sediment and macrophyte type from the still images taken of the seabed. Two divisions of the Wentworth grain scale (Wentworth 1922) were used to classify sediment type (Connor et al. 2004). A total of 66 (11 \times 6) randomly stratified points were overlaid on the image during CPC analysis following similar protocols used by Deter et al. (2012). Using the outputs from the CPC analysis, substratum categories were assigned based on the most dominant substrata occurring within each sample (Table 1), as per Elliott et al. (2016a). Substratum categories consisted of algal–boulder–cobble (ABC),

Table 1. Substratum type characterisation

Substratum type	Sediment composition	Particle size (cm)	Macrophyte type and density
Algal–boulder–cobble (ABC)	Boulders and cobbles	>6.4	Sediment covered in a mixture of kelp and red algae (>60%), e.g. <i>Laminaria</i> spp. and <i>Ceramium</i> spp.
Algal–gravel–pebble (AGP)	Gravel (stone, shell and maerl <i>Phymatolithon calcareum</i>) and pebble	~1.6–6.4	Between 20 and 50% cover by algae
Seagrass	Sandy sediment	~0.1–0.4	Presence of seagrass <i>Zostera marina</i>
Sand	Sandy sediment	~0.1–0.4	Absence of macrophytes
Mud	Mud and sandy mud sediment grain size	<0.1	Absence of algae

algal–gravel–pebble (AGP), seagrass *Zostera marina*, sand and mud (Table 1). Maerl was not treated separately as a result of its gravel–pebble-sized form around South Arran. Furthermore, impacted maerl has been demonstrated to be more similar to gravel than live maerl (Kamenos et al. 2003).

Data analysis

Permutational multivariate analysis of variance (PERMANOVA) was performed in PERMANOVA 6 software (Anderson et al. 2008) to investigate community composition differences in epibenthic and demersal fauna within and between substratum types. To explore community composition differences, the MaxN of epibenthic and demersal fauna were fourth-root transformed, to reduce the influence of dominant species (Clarke & Green 1988). Prior to applying PERMANOVA, a Bray-Curtis similarity coefficient was performed. Posterior pair-wise tests were used to compare the difference between substratum categories. PERMANOVA was run with 9999 permutations and results were considered significant at $p(\text{perm}) < 0.01$. Non-metric multi-dimensional scaling (nMDS) plots were used to visualise differences in epibenthic and demersal fauna between substratum types. nMDS plots provide a stress values that increase with reduced dimensionality or ordination (Clarke & Warwick 2001). Similarity percentages (SIMPER) analysis was used to determine species that contributed most to the dissimilarity between the different substratum types (Clarke & Warwick 2001).

To identify gadoid habitat variables, the abiotic variables explored included substratum type (categorical, 5 levels), depth (m), distance from coast (m), wave fetch (km) and year (categorical, 2 levels). Year was included in the model due to slight differences in sampling between years. The effect of epibenthic and demersal fauna MaxN was explored by Shannon-Wiener entropy (Jost 2010). To facilitate comparability between units, continuous explanatory variables were standardised by dividing the mean by the standard deviation prior to statistical analysis. Random effects used included the effect of the zones and grouped days of data collection where significant. Depth data were obtained from vessel echosounders. Distance from coast was calculated using the GPS fix made at the time of deployment and ArcGIS version 10.1 (EDINA digimap). Wave fetch values for a 200 m coastline grid (www.sams.ac.uk/michael-burrows/downloads) were used as described in Burrows et al. (2008).

Univariate statistical analysis was performed with the software R (version 3.2.1; R Core Team; www.r-project.org). Data exploration followed recommendations from Zuur et al. (2010). Homogeneity and potential outliers were analysed with boxplots. Variance inflation factor analysis and Spearman's rank correlations were used to test for collinearity. Temporal autocorrelation was accounted for by including year in the statistical model and day of collection as a random effect. Spatial independence was evaluated with variograms using R package geoR (<http://CRAN.R-project.org/package=geoR>). No spatial autocorrelation was observed. The model of best fit for all count data was a negative binomial distribution to account for over dispersion, using R package glmmADMB (<http://glmmadmb.r-forge.r-project.org/>). Backwards stepwise model selection was implemented (Bolker et al. 2009, Zuur et al. 2010), looking for potential interactions. Model selection and significance was tested using a log-likelihood ratio test. Pearson's residuals were compared between models, fitting a model with the highest level of heteroscedasticity. Tukey tests using R package multcomp (Hothorn et al. 2008) were performed to test for differences between categorical variables.

Eq. (1) provides the model structure used to explore juvenile gadoid habitat:

$$\log(Y_i) = \beta_0 + \beta_1 X_{ij} + \beta_2 X_i + \beta_3 X_i \dots + z_{ij} + t_{ij} \quad (1)$$

where Y_i is the gadoid MaxN, β are the coefficients, X are the explanatory variables, z_{ij} and t_{ij} are the random effects (zone and day of collection, respectively), i represents continuous-variable samples and ij represents categorical-variable samples.

Differences in substratum association between years was analysed via Eq. (2):

$$\log(Y_i) = \beta_0 + \beta_1 S_{ij} + \beta_2 Y_{ij} + z_{ij} \quad (2)$$

where S_{ij} is the substratum type and Y_{ij} is the year.

The habitat variables described above and day of the year were used to explore for any size-related differences in age-0 gadoids, enabling inferences on the quality of the habitat to be made (Gibson 1994, Able 1999, Elliott et al. 2016b). To reduce the likelihood of including age-1 gadoids, all individuals larger than 15 cm were removed from the analysis following Database of Trawl Surveys (DATRAS) ALK (product for standard species only) quarter 4 (October–December) data for the Clyde area (www.datras.com). Linear mixed models were employed using the R package nlme (<http://CRAN.R-project.org/package=nlme>) for length measurements:

$$Y_i = \beta_0 + \beta_1 D_{ij} + \beta_1 X_i \quad (3)$$

where Y_i is the gadoid fork length and D is day of the year.

To investigate whether the ability to identify and measure gadoids decreased with increasing depth (and therefore possibly reduced light), an ANOVA test was used to confirm that the ability to identify and measure gadoids did not decrease with depth.

RESULTS

Community composition substratum differences

Over the course of data collection, a total of 6186 epibenthic and demersal individuals from 65 species were recorded from the SBRUV deployments. Significant differences in community composition between substratum types were observed (pseudo- $F = 6.53$, $p(\text{perm}) < 0.0001$). Table 2 shows significant pair-wise test differences between substratum types and SIMPER percentage dissimilarity between substratum types and species. The nMDS plot had a stress value of 0.21 (relatively low), illustrating differences between the substratum types with some overlap (Fig. 3).

Gadus morhua habitat

An increase in MaxN was observed with increasing Shannon-Wiener entropy. A decrease in MaxN was observed with increasing depth and wave fetch (Fig. 4). Fewer *G. morhua* were observed in 2014 than 2013 (Table 3). Since no *G. morhua* were ob-

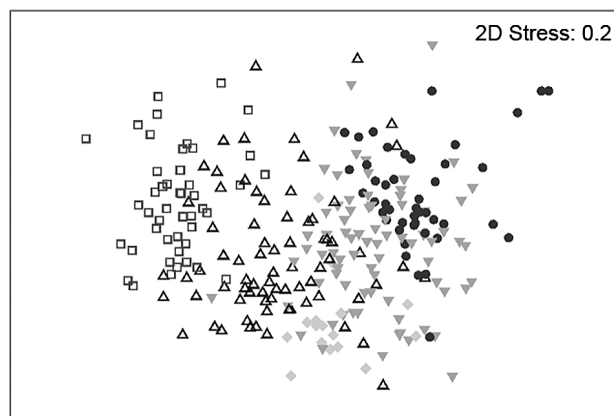


Fig. 3. Non-metric multi-dimensional scaling ordination plot (fourth-root transformation with Bray Curtis resemblance matrix) of mobile fauna observed over the different substratum types (□, algal-boulder-cobble; Δ, algal-gravel-pebble; ◆, seagrass; ▼, sand; ●, mud). Significant effects of substratum type on assemblage structure were observed (PERMANOVA, $p < 0.001$)

served over mud, this category was removed from the analysis to improve logistic model convergence. The highest MaxN was observed over AGP and the mean average MaxN was observed over sand ($l = -310.99$, $df = 10$, $\theta = 1.09$, $p < 0.001$; Figs. 4 & 5). A significant difference in MaxN across substrata and year was observed. During both years, higher *G. morhua* MaxN was observed over AGP than other substrata. In addition, mean MaxN observed over AGP remained relatively constant, whereas it decreased over other substrata ($l = -331.36$, $df = 10$, $\theta = 1.09$, $p < 0.001$; Fig. 5).

Table 2. Pairwise tests and percentage dissimilarity in epibenthic and demersal fauna assemblage composition between substratum type. PERMANOVA was run 9999 times and results were considered significant at $p(\text{perm}) < 0.01$. AGP, algal-gravel-pebble; ABC, algal-boulder-cobble

Substratum types	t statistic	$p(\text{perm})$	Unique perms	Dissimilarity (%)	Top 3 species causing dissimilarity
AGP, sand	2.16	0.05	9945	79	<i>Gadus morhua</i> , <i>Melanogrammus aeglefinus</i> , flatfish Pleuronectiformes
AGP, seagrass	5.10	0.01	9962	73	Pleuronectiformes, shore crab <i>Carcinus maenas</i> , <i>G. morhua</i>
AGP, ABC	4.24	0.00	9933	77	Goldsinny <i>Ctenolabrus rupestris</i> , <i>G. morhua</i> , two-spotted goby <i>Gobiusculus flavescens</i>
AGP, mud	3.51	0.05	9868	82	<i>G. morhua</i> , rugose squat lobster <i>Munida rugosa</i> , <i>Merlangius merlangus</i>
Sand, ABC	4.57	0.00	9949	90	<i>C. rupestris</i> , <i>M. aeglefinus</i> , harbour crab <i>Liocarcinus depurator</i>
Sand, seagrass	2.42	0.01	9966	68	<i>C. maenas</i> , <i>M. aeglefinus</i> , <i>G. morhua</i>
Sand, mud	3.55	0.05	9852	67	<i>M. rugosa</i> , <i>M. merlangus</i> , <i>M. aeglefinus</i>
ABC, seagrass	6.43	0.00	9939	87	<i>C. rupestris</i> , Pleuronectiformes, <i>L. depurator</i>
ABC, mud	4.77	0.00	9849	95	<i>C. rupestris</i> , <i>M. rugosa</i> , <i>M. merlangus</i>
Seagrass, mud	3.29	0.01	4378	78	<i>M. rugosa</i> , <i>C. maenas</i> , <i>G. morhua</i>

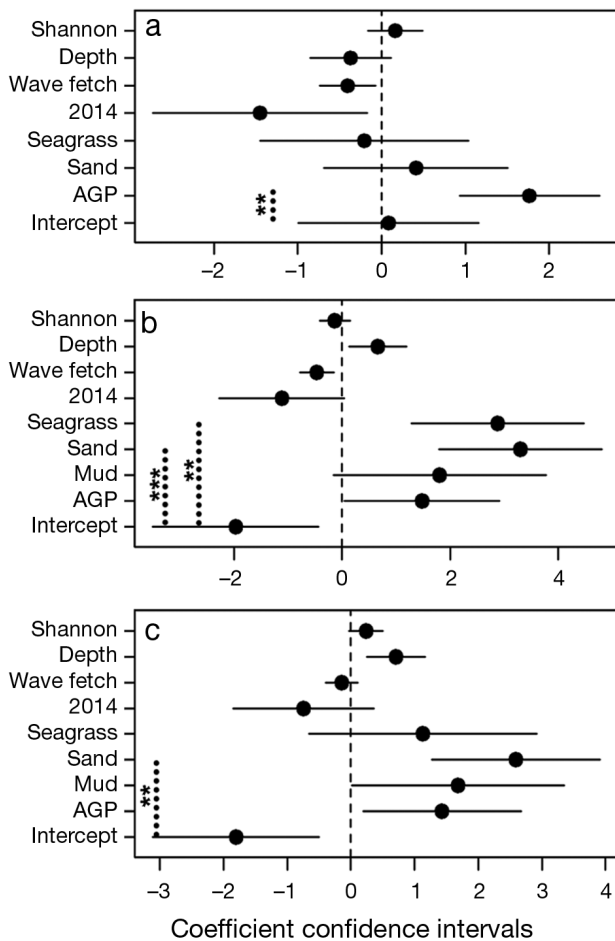


Fig. 4. Coefficient plot for model of best fit for (a) *Gadus morhua*, (b) *Melanogrammus aeglefinus* and (c) *Merlangius merlangus* habitat variables. Lines are the 95% confidence intervals for each of the explanatory variables. The continuous vertical dashed line is the reference line enabling us to see which coefficients are significantly different from zero. The intercept represents algal–boulder–cobble and year 1 (2013) of data collection, AGP refers to algal–gravel–pebble. Dotted vertical lines with * refer to Tukey test p-value significance between substrata: ** $p < 0.01$, *** $p < 0.001$)

During field season 2013, an increase in length was observed, as well as an increase in length with Shannon-Wiener entropy ($l = -248.49$, $df = 7$, $p < 0.001$; Table 4). Significantly larger *G. morhua* were observed over AGP (7.5 cm, $SE \pm 0.03$ cm) than sand (5.7 cm, $SE \pm 0.1$ cm) ($p < 0.05$; Fig. 6). During field season 2014, a significant increase in length was observed over the period of data collection (Table 4). Significantly larger *G. morhua* were observed over seagrass (10.2 cm, $SE \pm 0.1$ cm) than AGP (7.8 cm, $SE \pm 0.03$ cm) ($l = -188.33$, $df = 5$, $p < 0.05$; Fig. 6).

Melanogrammus aeglefinus habitat

An increase in *M. aeglefinus* MaxN was observed with increasing depth. A decrease in MaxN was observed with increasing wave fetch and Shannon entropy (Fig. 4). More individuals were observed in 2014 than 2013 (Table 3). The highest MaxN for *M. aeglefinus* was observed over the sand with lowest MaxN observed over ABC ($l = -279.92$, $df = 11$, $\theta = 1.33$, $p < 0.001$; Fig. 5).

Due to differences in data collection between years, it was not possible to undertake statistical analysis comparing *M. aeglefinus* MaxN between substratum type, since no data were collected in deeper water containing mud in year one. Over the course of both years, few individuals were observed in ABC and consistently greater numbers of *M. aeglefinus* were, however, observed over sand (Fig. 5).

A significant increase in length was observed over the course of data collection during 2013 ($l = -88.19$, $df = 3$, $p < 0.001$; Table 4). During field season 2014, a significant increase in length was observed over the course of data collection in addition to increasing length with depth and wave fetch ($l = -221.93$, $df = 7$, $p < 0.001$; Table 4).

Table 3. Juvenile gadoid MaxN summary results. Arrows represent an increase or decrease in gadoid MaxN

Species	Year	Total number of individuals measured at MaxN	Mean MaxN \pm SE	Habitat variable effect for both 2013 and 2014	Substratum significant difference for both 2013 and 2014
<i>Gadus morhua</i>	2013	268	3.62 \pm 0.44	Shannon \uparrow	AGP–ABC
	2014	182	1.31 \pm 0.38	Depth \downarrow Wave fetch \downarrow	
<i>Melanogrammus aeglefinus</i>	2013	64	0.86 \pm 0.37	Shannon \downarrow	Sand–ABC Seagrass–ABC
	2014	190	1.03 \pm 0.15	Depth \uparrow Wave fetch \downarrow	
<i>Merlangius merlangus</i>	2013	30	0.40 \pm 1.02	Shannon \uparrow	Sand–ABC
	2014	192	1.05 \pm 2.18	Depth \uparrow Wave fetch \downarrow	

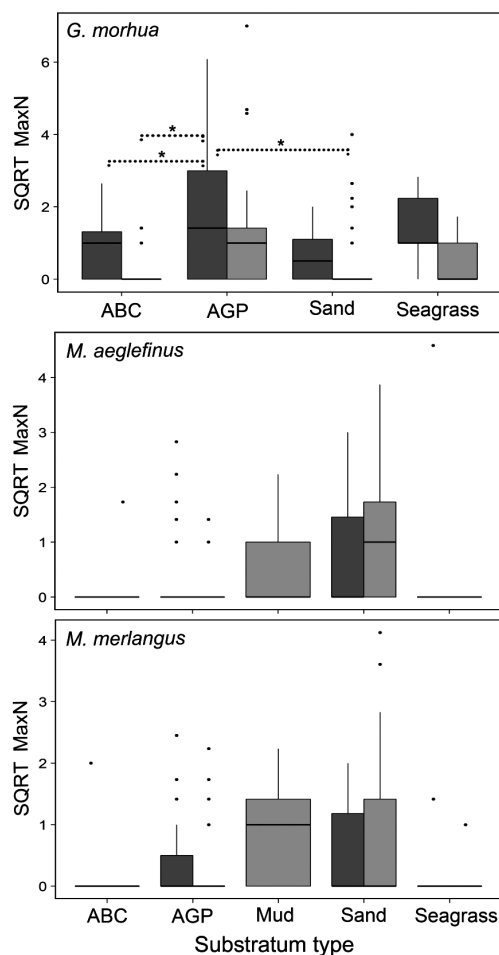


Fig. 5. Substratum association between data collection period 2013 (dark grey) and 2014 (light grey) for juvenile *Gadus morhua*, *Melanogrammus aeglefinus* and *Merlangius merlangus* observed within South Arran Nature Conservation Marine Protected Area. Boxplots: 25th and 75th percentiles of the total number of juvenile gadoids observed within the different substrata; upper and lower whiskers: 10th and 90th percentiles; thick horizontal line: median MaxN; solid dots: outliers. Dotted horizontal lines with * refer to Tukey test p-value significance between substrata ($p < 0.05$). ABC, algal-boulder-cobble; AGP, algal-gravel-pebble

Merlangius merlangus habitat

An increase in MaxN was observed with increasing Shannon-Wiener entropy and depth and a decrease in MaxN was observed with increasing wave fetch (Fig. 4). Fewer individuals were observed in 2013 (Table 3). The highest MaxN for *M. merlangus* was observed over sand with the lowest MaxN observed over ABC ($t = -273.64$, $df = 11$, $\theta = 1.17$, $p < 0.001$; Figs. 4 & 5). More *M. merlangus* was observed over sand substrata than the other substrata over the 2 years of data collection (Fig. 5).

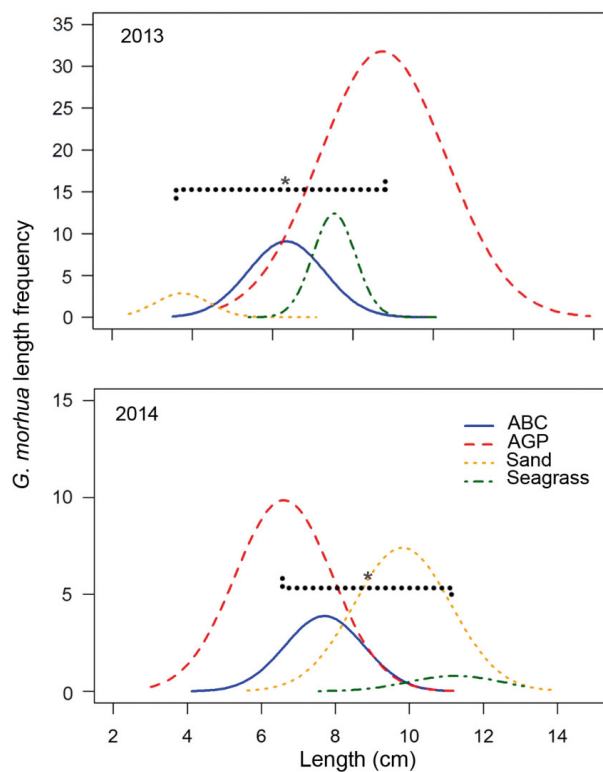


Fig. 6. Length-frequency distributions by substratum for *Gadus morhua* during 2013 and 2014. Year 2013 illustrates that *G. morhua* were significantly larger over algal-gravel-pebble (AGP) than sand. During year 2014 *G. morhua* was significantly larger over seagrass than AGP. ABC refers to algal-boulder-cobble. Dotted horizontal lines with * refer to Tukey test p-value significance ($p < 0.05$)

During field season 2013, a significant increase in length was observed ($t = -15.56$, $df = 4$, $p < 0.05$; Table 4). During field season 2014, an increase in length with increasing depth was observed ($t = -188.29$, $df = 3$, $p < 0.01$; Table 4).

DISCUSSION

There is a paucity of data on the habitat requirements of commercially important gadoids (*Gadus morhua*, *Melanogrammus aeglefinus* and *Merlangius merlangus*) within Eastern Atlantic waters. Our study provides information on the relationship between juvenile gadoid habitat variables from SBRUV field observations during daylight hours. A variety of habitat variables (5 substratum types, depth, wave fetch and Shannon-Wiener entropy) affected the distribution of these gadoids, demonstrating the importance of exploring abiotic and biotic factors that affect the distribution of species. It was observed that

Table 4. Gadoid age-0 (<15 cm) length measurements and ontogenetic shift changes. na: not applicable

Species	Year	Number of length measurements	Mean length (cm) \pm SE	Minimum size observed (cm)	Length increase significance	Ontogenetic shift significance
<i>Gadus morhua</i>	2013	123	7.4 \pm 0.2	2.4	<0.001	Shannon <0.05 Substratum type <0.05
	2014	96	8.3 \pm 0.2	3.0	<0.001	Substratum type <0.05
<i>Melanogrammus aeglefinus</i>	2013	50	12.3 \pm 0.2	7.6	<0.001	na
	2014	131	10.6 \pm 0.1	6.7	<0.001	Depth <0.001 Wave fetch <0.05
<i>Merlangius merlangus</i>	2013	9	10.7 \pm 0.7	8.3	<0.05	na
	2014	83	11.3 \pm 0.2	6.3	>0.05	Depth <0.01

the niche occupation of *G. morhua* was distinct from that of *M. aeglefinus* and *M. merlangus*. Furthermore ontogenetic shifts in the distribution of age-0 individuals were observed for a size range of 3–15 cm.

Over both years of data collection, a greater relative abundance of *G. morhua* was observed over the AGP substratum type, with no individuals observed over mud and the fewest individuals observed over sand. These results support previous observations collected by stereo-video SCUBA transects (Elliott et al. 2016a). It is likely that fewer *G. morhua* were observed over seagrass areas due to the patchy, low density and small area (less than 1 km²) of seagrass (Jackson et al. 2001, Gorman et al. 2009, McCloskey & Unsworth 2015) around South Arran (Elliott et al. 2016a). Fewer *G. morhua* may have been observed over ABC substrata as other potential predatory fish were observed around these areas e.g. age-1+ pollack *Pollachius pollachius* and saithe *Pollachius virens*. Similar laboratory results were observed by Gotceitas & Brown (1993), where in the absence of predators, juvenile *G. morhua* were observed over gravel-pebble; however, in the presence of predators, they hid in the interstitial spaces of cobble. Much of the gravel where the SBRUV deployments took place around South Arran contained maerl. Maerl is thought to contribute to higher species diversity and heterogeneity and may be of importance to juvenile *G. morhua* (Hall-Spencer et al. 2003, Kamenos 2004).

During data collection period 2014, where significantly fewer *G. morhua* were observed, its relative abundance was reduced over all substrata apart from AGP where the *G. morhua* relative abundance remained more constant. This could be evidence of selection of AGP, with density-dependent dispersal to other substrata at higher population densities. This indicates that this substratum could be an important seabed type for juvenile *G. morhua* (Morris 1989,

2003, Swain & Wade 1993). Lough (2010) also indicated that limited gravel areas may inhibit the survival of juvenile *G. morhua*. Juvenile *G. morhua* density-dependent substrata association was likewise observed by Laurel et al. (2004), who found that the abundance of *G. morhua* was consistently high over seagrass areas and more variable in sand.

Over the period of data collection, ontogenetic shifts in substratum association were observed. An increase in age-0 *G. morhua* relative abundance was observed over more structurally rugose substrata relative to their size. Keats & Steele (1992), Laurel et al. (2007) and Tupper & Boutilier (1995b) also observed ontogenetic shifts to more rugose substrata with increased size. Older (age-1+) and larger gadoids have, however, been observed to move into deeper, less rugose substrata with size (Cote et al. 2008, 2013, Munsch et al. 2016). Ontogenetic shifts within the size range observed highlights the importance of substrata of sufficient rugosity relative to the size of the individual and that multiple substratum types may be needed by the same species (Nagelkerken et al. 2013, Elliott et al. 2016b). Differences between years (2013 and 2014) may be due to on average larger individuals recorded in 2014 than 2013. In addition, in 2014, sampling took place at a larger range of depths than in 2013.

Although previous research has suggested that *M. aeglefinus* and *M. merlangus* do not seem to have a particular nursery grounds (Hislop 1996), significant substratum associations were observed. In contrast to *G. morhua*, higher relative abundances of both *M. aeglefinus* and *M. merlangus* were observed over sand followed by mud, with the fewest individuals observed over ABC substrata. Higher relative abundance over sand was also observed for both years of data collection for both species, indicating a selection for this substratum type. These results match laboratory and field studies undertaken with *M. merlangus*

and *M. aeglefinus* (Auster et al. 2001, Atkinson et al. 2004). *M. aeglefinus* and *M. merlangus* also demonstrated ontogenetic shifts to deeper waters with increasing size. Such results demonstrate that measures to protect juveniles must be tailored to the species and life-history stages under consideration, and that there may not be general rules that apply evenly within groups of closely related fish (Nagelkerken et al. 2013).

Similarities in substratum association between *M. aeglefinus* and *M. merlangus* may be because, on average, *M. aeglefinus* and *M. merlangus* were similar in size, and individuals of both species were larger than *G. morhua*. Such size-related behaviour may reduce agonistic interactions, such as competition for resources between individuals and/or predation from larger individuals (Keats & Steele 1992, Cote et al. 2008, Bastrikin et al. 2014). Species-specific segregation potentially reduces predation (Myers & Cadigan 1993, Fromentin et al. 1997) and minimises competition, most likely as a result of different resource needs (Fromentin et al. 1997, Bastrikin et al. 2014).

The relative abundances of *G. morhua* and *M. merlangus* were positively correlated with Shannon-Wiener diversity entropy. This indicates that *G. morhua* and *M. merlangus* are found in higher relative abundance when epibenthic and demersal fauna composition is more even (where an increased ratio of the number of species relative to the total number of individuals is observed) (Hill 1973, Jost 2010). Maintaining species biological diversity is a well-known mechanism for maintaining the ecosystem services on which we depend (Worm et al. 2006, Beaumont et al. 2008).

Growth rates are also used as an indicator for the quality of a habitat (Gibson 1994, Searcy et al. 2007, Elliott et al. 2016b). This is particularly relevant in the case of *G. morhua*, where an increase in growth was correlated with an increase in epibenthic and demersal fauna diversity. More diverse areas can be assumed to represent higher-quality habitats. Declines in species diversity are largely caused by anthropogenic impacts such as exploitation, physical damage to substrata and pollution (Thrush & Dayton 2002, Lotze 2006, Worm et al. 2006).

Much of the maerl found around South Arran is degraded as a result of historic dredging activity (Thurstan & Roberts 2010). Shallower gravel-type substrata containing maerl, where *G. morhua* were found in greater relative abundance, could be more vulnerable to dredging activities that take place in these shallower areas (Collie et al. 2000, Kaiser et al.

2006). Protecting more biodiverse areas may support the survival of commercial fish (Worm et al. 2006, Beaumont et al. 2008).

Wave exposure has previously been identified as having a strong influence on the local distribution of coastal species (Burrows et al. 2008, Burrows 2012). For all 3 gadoids, a negative relationship between their relative abundance and wave fetch was observed. Fromentin et al. (1997) also observed higher abundances of *G. morhua* and *M. merlangus* in more sheltered areas within fjords as opposed to more exposed areas outside fjords. These results differ from the results of Lekve et al (2006), who found an increased abundance of *G. morhua* in more exposed areas. This is another example of the variability in natural history between *G. morhua* across its range.

Few studies have been undertaken using SBRUV as a mechanism to collect fisheries-independent data in the Europe. The findings within this study linking gadoid relative abundance to their habitats using SBRUV deployments within UK coastal waters have relevance across the region. With the increasing number of spatial closures being designated within European waters, SBRUV surveys could be used as a fisheries and marine protected area (MPA) monitoring method in a variety of conditions and seabed types, supporting more ecosystem-based management.

In conclusion, this study demonstrates the importance of taking into consideration a range of habitat variables to better understand demersal fish distribution. The link between epibenthic and demersal species diversity has significant management implications since insufficient good-quality habitat may be causing recruitment bottlenecks due to the carrying capacity of the environment (Svåsand et al. 2000). This has MPA and Marine Strategy Framework Directive (MSFD, 2008/56/EC) management and monitoring implications given that the descriptors linking together biodiversity (D1), seafloor integrity (D6) and commercially exploited fish (D3) indicators have not yet been addressed. We recommend linking commercially exploited fish during critical life phases to habitat variables to support the recovery of depleted fish stocks and implement more ecosystem-based management. By understanding the range of conditions suitable to gadoid species, adequate protection measures can be implemented to try to recover stocks through improved habitat quality.

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